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PREFACE

The success of the *Annual Review of Entomology (ARE)* has been measured by the number of times its chapters are cited in the scientific literature, and it is indeed the most cited entomology periodical. However, and perhaps fortunately, the need to know is not necessarily correlated with the need to cite. In this regard, *ARE* provides a wealth of information that has always been most useful to me as a lifelong student and as a teacher: From what angle do my peers see "the big picture" in a field that I thought I knew, and what new directions of research will they generously expose? And what is known of that distant topic that I have never explored, and what are the challenging concepts that should attract me to it?

The Editorial Committee of *ARE* has the privilege to select topics for the *Review* and thereby possibly influence the development of entomology in a way that a primary-research publication cannot. Of the hundreds of topics discussed, few are selected, but it is the diversity of suggestions from Committee members, our International Correspondents, and our authors, as well as from readers at large, that makes the choice of a balanced complement of reviews possible. I conclude my term on the Committee by thanking all those who have made this responsibility lighter—the Editors and Committee members for sharing their experience and their views with me.

Because insects have attracted scientists from so many disciplines, it is perhaps not surprising to find, year after year, chapters devoted to insects in many other Annual Review series (for instance the *Annual Reviews of Biochemistry, Ecology and Systematics, Fluid Mechanics, Genetics, Microbiology, Neuroscience, Physiology, Phytopathology,* and, yes, *Earth and Planetary Sciences;* see lists of Other Reviews of Entomological Interest in the preliminary pages of previous *ARE* volumes). This is a welcome situation, because the problems that insects cause or the problems that insects have solved are now studied more urgently, more widely, and more successfully than ever before. In this sense, Entomology has now truly become Insect Science.

On behalf of the Editorial Committee, I thank the authors of Volume 38 and Amanda Suver, our Production Editor, for their contributions, efforts, and dedication.

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RENÉ FEYEREISEN
FOR THE EDITORIAL COMMITTEE

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PERSPECTIVES AND OVERVIEW

The success of an individual organism is commonly assessed in terms of the number of viable offspring it contributes to the next generation. For an animal to leave any offspring, it needs to find and utilize different kinds of resources and must avoid death or debilitation before reproducing. In obtaining the necessary resources for reproductive success and in avoiding hazards, most animals need to display a number of behaviors and respond to a multiplicity of stimuli. In general terms, the complexity of an animal's resource-oriented behavior, and the number of resource-related stimuli to which it must be able to respond, increase commensurately with the number of different resources it requires and the extent to which these are spatially separated.

In insects, the number of resources required, and hence the complexity of resource-oriented behavior, varies according to the stage of development and sex of an individual, and between species. Food is a resource required by the larvae of all species and the adults of most, but only adults need resources specifically related to reproduction. The adult male needs to acquire at least one mate as does the female, unless she is parthenogenetic. The female also needs a suitable site for the deposition of eggs or living offspring. Variation between species is very wide indeed. At one extreme are the parthenogenetic, apterous aphids, which usually spend their whole lives on one plant that supplies all nutrients and the site for deposition of living offspring. The only

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resource-oriented behavioral requirement is that the aphid can change its position on the plant to obtain a more favorable site for feeding or larviposition. At the other extreme, an insect such as the adult, anautogenous female mosquito needs several kinds of spatially separated resources: a mate, two distinct categories of food, and an oviposition site. Such insects often need to display a range of resource-oriented locomotor behaviors in addition to behaviors that enable them to utilize resources, once these have been located.

It has long been recognized that the responsiveness of insects to specific stimuli, as well as the likelihood that they will display spontaneous behavior, is modulated by endogenous factors, and that these cause insects in the same situation to behave in different ways at different times (53, 54, 89, 90). The influence of endogenous factors on the readiness of insects to engage in any particular behavior is the basis for their ability to order their resource-oriented behaviors throughout their lives and over the diel cycle and to integrate these behaviors with those concerned with the avoidance of environmental hazards.

In insects, as in other animals, all behavior is the outcome of physiological processes in the nervous, endocrine, and muscular systems. Physiology can thus be considered to influence all aspects of resource-oriented behavior. This article is, however, restricted to a consideration of the ways in which the physiological state of an insect can influence its readiness to acquire three major resources required for reproductive success—food (including water), mates, and oviposition sites—and how changes in readiness to engage in these behaviors can determine an insect's behavioral priorities at any given time.

FOOD-ORIENTED BEHAVIOR

This section discusses how an insect's stage of somatic or reproductive development and its nutritional state affects behavior directed towards the acquisition of nutriment. Other significant endogenous factors known to influence food-oriented behavior are (a) diapause (26, 170), (b) short-term effects of excitatory (10, 36, 56, 188) or inhibitory (57) sensory input, (c) short-term effects of behavior itself (91), (d) learning (98, 99 and references therein), and (e) circadian rhythmicity (28, 31).

Effects of Stage of Development

Stage of somatic or reproductive development influences both rate of intake measured over a period (e.g. amount of food consumed per day) and preferences for particular kinds of food. Changes within and between larval instars and those related to states of somatic and reproductive development in adults are discussed.

CHANGES DURING LARVAL DEVELOPMENT   The temporal pattern of changes in rate of intake within an instar is probably generally similar in most insects.

Following a molt, the intake rate first increases (e.g. 37, 133, 152) then declines, with feeding ceasing at some time before the next molt (e.g. 37, 187, 199). The initial increase may result from increased duration of meals as in the final instar of the hornworm *Manduca sexta* (133), from increased frequency of feeding as in the first instar of the grasshopper *Schistocerca americana* (37), or largely from increased rate of ingestion during meals as in the final instar of the locust *Locusta migratoria* (152). Thus, in the first two cases, but not markedly in the third, the proportion of time devoted to feeding behavior rises progressively over the first part of the instar. In the period preceding a molt, food-oriented behavior effectively disappears from the insect's behavioral repertoire.

Food preference can change within an instar. Larvae of the cockroach, *Supella longipalpa*, prefer a diet containing carbohydrate and no protein over one containing protein and no carbohydrate early in each of the two instars examined but consume equal quantities of the two diets later in these instars (43). The final instar of the lepidopteran *Heliothis zea* exhibits the opposite trend (45).

Throughout larval life, rate of intake increases from instar to instar (e.g. 33, 110, 131), but there is a general paucity of detailed information on the behavioral basis for such interinstar changes. However, the proportion of time spent feeding has been shown to be generally similar in all five instars of *H. zea* (1), which indicates that the increase in intake rate in successive instars is the result of increasing ingestion. Different instars of some phytophagous species feed on different parts of host plants (e.g. 44, 138), indicating that the stages have different food preferences.

CHANGES DURING THE ADULT STAGE Some insects undergo substantial somatic development after adult eclosion, and the food intake of several species is high during this phase. One can most clearly see this trend in males, in which it is less obscured by patterns of intake related to reproductive development. For example, intake rates of males of the locusts *Schistocerca gregaria* (194) and *L. migratoria* (172) and the milkweed bug *Oncopeltus fasciatus* (162), throughout some days following eclosion, are very much greater than later. In addition, the food preferences shown by males during the teneral period can differ from those exhibited later in life.

In females, behavior directed towards the acquisition of food types needed to support ovarian development is influenced by reproductive condition. Effects are particularly striking in insects that display distinct ovarian cycles in which intake of such foods, or responsiveness to sensory cues associated with them, declines in each ovarian cycle, as the synchronously developing oocytes approach or reach maturity. Food intake by the cockroaches *Leucophaea maderae* (61) and *Blattella germanica* (42, 76) is high during maturation of a batch of oocytes, and falls at about the time of ovulation to

a low level, at which it remains until *L. maderae* deposits living young or *B. germanica* deposits the ootheca just prior to egg hatch. Intake of protein-rich material by females of the blowflies *Phormia regina* (13, 52) and *Lucilia cuprina* (137) and the face fly *Musca autumnalis* (185), with ad libitum access to solutions of protein and sucrose, declines as each batch of oocytes approaches maturity. Analogous changes occur in female tsetse (*Glossina* spp.), which are viviparous and feed only on mammalian blood (46). In these insects, the size of blood meal declines sharply during the few days before larviposition (179). Gravid female mosquitoes are unresponsive to odors associated with mammalian hosts (26, 92). Investigation of the physiological bases for the influence of stage of reproductive development on nutrient-oriented behavior has revealed the involvement of ovary- and fat body–produced humoral factors in mosquitoes (26, 92) and probably neural input concerning the amount of abdominal distension in blowflies (12, 16) and tsetse (179).

Intake rates of females also vary in more general ways in relation to the requirement for nutrient to support ovarian development. Virgin females of many insects lay fewer eggs than mated ones (see below), and in several species, e.g. *O. fasciatus* (162), the cricket *Acheta domesticus* (198), and the housefly *Musca domestica* (73), virgins consume less food than mated individuals. Females of some species or races of dipterans can develop their first batch of oocytes without ingesting protein-rich material after eclosion but require protein for subsequent ova. in cycles. Typically these insects direct less behavior toward the acquisition of protein in the first than in than later ovarian cycles (e.g. 108, 116, 168).

Food preference by females is also affected by their reproductive state. Postteneral females of *S. gregaria* given access to lettuce and bran select a diet higher in protein content than during somatic development (113). The results referred to earlier for female blowflies with access to solutions of protein and sugar (52, 137) can also be viewed as changes in preference between the two kinds of solution, because the intake of protein relative to that of sugar declines as each batch of oocytes approaches maturity.

Effects of Nutritional State

Nutritional state influences the readiness of an insect to engage in behavior directed towards the acquisition of any kind of nutriment and affects food preference. A considerable amount of information is now available about the physiological basis for the effects of the nutritional state of insects on their food-oriented behavior, and a range of neural and hormonal mechanisms involving volumetric and nutritional feedback has been identified (see 8, 17, 19, 20, 55, 153, 156, 160 for detailed discussions).

EFFECTS OF DEPRIVING INSECTS OF ALL FOODS   Several studies have exam-

ined the effects of total food-deprivation on various facets of food-oriented behavior. Not surprisingly, these have commonly shown that food-deprived insects behave in ways that enhance their likelihood of encountering and ingesting food. Generally, such insects are more responsive than recently fed ones to olfactory (e.g. 112, 191), visual (e.g. 27, 80), and gustatory (e.g. 25, 55, 60, 66, 174) cues provided by food. The size of the first meal taken by an insect after enforced deprivation has been shown to be positively correlated with the deprivation period (e.g. 18, 22, 67), and insects that have been subjected to prolonged food deprivation can show elevated rates of intake that extend beyond the first post-deprivation meal (24, 83, 140, 186). In addition, the degree of deprivation can affect two aspects of locomotor behavior. First, the level of spontaneous locomotor activity is often greater in food-deprived insects than in recently fed ones, over at least moderate periods of enforced deprivation (e.g. 5, 27, 72, but see 132, 140). Second, deprivation can cause an increase in the duration of what has been termed local search (14), a behavior shown by some species in which the insect, for a time after having contacted food without ingesting it or having consumed an amount insufficient to cause satiation, shows increased rates of turning and moves more slowly than before the encounter.

EFFECTS OF DEPRIVING INSECTS OF PARTICULAR NUTRIENTS   The feeding preferences of larvae of *L. migratoria* and the lepidopteran *Spodoptera littoralis* are strongly modified by a period of feeding on diets deficient in one category of nutrients (158, 159). A period of feeding on artificial diet containing only carbohydrate and no protein shifts the preference of both insects towards diet containing protein but no carbohydrate when given a choice between that diet and their previous diet. Conversely, enforced feeding on diet containing protein but no carbohydrate shifts preference towards diet containing carbohydrate but no protein. The shift is especially striking in the case of protein-deprived locust larvae, which show enhanced preference for the diet containing protein but no carbohydrate after having taken only a single meal of protein-deficient diet (159). Recent research has established that the behavioral basis for these preferences by larvae of *L. migratoria* is that most insects rapidly reject the nutritionally deficient diet to which they previously had access, whereas most take a prolonged initial meal when they encounter the diet containing the nutrient that had been absent from their previous diet (157). Simpson & Simpson (160) discuss in detail the physiological bases for such shifts in preference between carbohydrate-deficient and protein-deficient diet. Also, an insect's state of hydration, as determined by its recent feeding history, can affect its food preference in an analogous way. When final-instar larvae of *S. gregaria* that have fed on either high- (seedling wheat leaves) or low- (lyophilized wheat leaves)

water-content food for several days are given a choice of the two kinds of food, the insects that previously fed on the wet food show a strong preference for the dry food, and vice versa (102).

AD LIBITUM FEEDING   Observations have been made on the food-oriented behavior of insects with continuous access to one kind of food that is nutritionally adequate, at least in that it supports survival. Detailed and continuous observations have been made, over a period of at least some hours, on the feeding behavior of three insects, the final-instar larvae of the locust *L. migratoria* (152) and of the hornworm *Manduca sexta* (23, 133, 178), and the adult male of the blowfly *L. cuprina* (155). Each of these insects alternates between bouts of ingestion (meals) and periods during which the insect does not feed even though in close proximity to or, in case of the caterpillar, in contact with food. These findings indicate that food-oriented behavior is effectively eliminated from the behavioral repertoire of these insects for a period after the ingestion of each meal. Simpson (153) has reviewed the relationships between observed patterns of feeding in acridids and knowledge of the mechanisms regulating their food intake.

Several studies with ad libitum–feeding insects have examined the effect of diluting a nutritionally adequate diet with water or a nonnutrient solid on intake rate over a period and, in some instances, on the temporal pattern of intake. Many species of insects increase the amount of food they consume in response to dilution (160, 163 and references therein, 197). Detailed observations have shown that insects feeding on dilute diets devote a higher proportion of their time to food-oriented behavior. A fourfold dilution of artificial diet with cellulose causes the proportion of total time spent feeding by final-instar larvae of *M. sexta* to increase from 10 to 25%, as a result of increases in both meal size and frequency (178). In adult males of *L. cuprina*, a 10-fold dilution of sucrose solution results in a fourfold increase in time spent feeding—from about 1 to 4% of total photophase (155). Compensatory increases in intake also occur in response to reduction in the amount of specific categories of nutrients. Larvae of *L. migratoria* and *S. gregaria* compensate strongly for reduction in the protein content in their diet and, to a lesser extent, for reduction in carbohydrate content (129, 154). In *L. migratoria*, a twofold reduction in protein content of the diet resulted in an approximately 1.5-fold increase in both intake and proportion of time spent feeding (154). Simpson & Simpson (160) discuss in detail the physiological and behavioral bases for compensatory feeding.

Larvae of *S. longipalpa* (43) and *H. zea* (45) with ad libitum access to two diets that are nutritionally deficient in complementary ways will consume some of each; the relative amounts consumed are such that development rate approaches the maximum possible. This phenomenon, which has been termed

dietary self-selection, was discussed in detail in two recent reviews (160, 192). Self-selection behavior implies that an insect can perceive deficiencies and modify its behavior in ways to increase the likelihood that it will ingest nutrients that will make up the deficiency. The behavioral mechanisms responsible for the preferences displayed by insects given the choice of two deficient diets after the obligatory consumption of one of them are probably central to self-selection behavior. Continuous observations of larvae of *H. zea* have shown that larvae supplied with two nutritionally incomplete diets switch frequently between them, whereas larvae supplied with two blocks of complete diet seldom switch (45). These findings suggest that larvae of this species display locomotor activity when they suffer a nutritional deficiency.

MATE-ORIENTED BEHAVIOR

A range of endogenous factors influences the readiness with which insects engage in mate-oriented or sexual behavior. Here, I consider only the effects of the insect's age, aspects of its nutrition, and its mating history. Other endogenous factors known to influence sexual behavior are circadian rhythmicity (e.g. 4, 63, 184) and effects of experience (126, 193).

Sexual behaviors fall into two general categories: those displayed in the absence of insects of the opposite sex and those that are induced by stimuli produced by the opposite sex. Two of the most important in the first category are sex-pheromone release by the female and the emission of acoustic signals by the male. Important facets of sexual behavior that fall into the second category are the responses of the male to female-produced sex pheromone, the responses of the female to male-produced acoustic signals and pheromones, a range of sexual behaviors directed by males toward females in their immediate vicinity, and responses by the female that determine whether she will mate when courted by a male.

Effects of Age and Nutrition

The time-course of the development of sexual behavior following adult eclosion varies markedly between species and between sexes in the same species. In some species, the onset of sexual behavior is affected by diet.

FEMALES Females of some species, including the the gypsy moth *Lymantria dispar* (58), the mosquito *Wyeomyia smithii* (121), and the leafminer *Agromyza frontella* (34), will mate very early in adult life, but those of many species do not mate for one or more days after eclosion. Some examples are the cricket *A. domesticus* (142), the locust *S. gregaria* (173), the grasshopper *Chorthippus curtipennis* (78), the cockroach *S. longipalpa* (41), the tsetse *Glossina pallidipes* (195), and some species of *Drosophila* (109, 200). Young

females might fail to mate because of one or both of two factors: lack of courtship by the male and lack of appropriate responses by the female to male courtship or attempts at copulation. Males can fail to direct sexual behavior towards young females because they fail to release or lack sex pheromones. Some studies showing that females do not mate until one or more days after eclosion do not clearly distinguish between the roles played in this failure by lack of courtship and lack of sexual receptivity of the female.

Females of some species, notably lepidopterans and cockroaches, release sex pheromone by means of active calling behavior. Species in which a high proportion of females release pheromone on the day of eclosion include the lepidopterans *L. dispar* (38) and *Epiphyas postvittana* (97). In some other lepidopterans, for example *Agrotis ipsilon* (176) and *S. littoralis* (59), 50% or fewer call on the day of eclosion; the remainder first do so on days 2 and 3. In other species, notably the moth *Pseudaletia unipunctata* (51) and the cockroach *S. longipalpa* (164), no females call on the day of eclosion; they begin to do so after one or more days. The development of calling behavior appears to be under hormonal control in some species, e.g. *P. unipunctata* (48) and *S. longipalpa* (164), but not in others including *L. dispar* (79) and *M. sexta* (144).

In some insects, notably some dipterans, sex pheromones are present on the cuticular surface of the female (21). In these instances, the availability of pheromone as an olfactory or gustatory stimulus for the male is independent of any overt behavior on the part of the female. In the housefly *M. domestica*, pheromone is known to be absent from the cuticle of newly emerged females, and some evidence suggests that this absence limits the amount of courtship directed toward young females (2). Blomquist et al (21) have reviewed the general topic of relation between female age and the amount of pheromone on the cuticle surface and the physiological processes regulating pheromone synthesis.

Lack of mating in young females of some species largely results from the female's failure to respond to male-produced sexual signals or to copulatory attempts by males. Females acting in these ways are categorized as unreceptive. Females of the cricket *A. domesticus* fail to respond positively to male acoustic signals for several days after eclosion (94). In the tephritids *Dacus tryoni* (63) and *Toxotrypana curvicauda* (96), females do not respond to male-produced sex pheromone for some days after eclosion. In many instances, however, mating fails to occur because females fail to respond appropriately to cues provided at short range by males during courtship. When courted, unreceptive females of the cricket *A. domesticus* do not mount the male and do not assume the copulatory position that allows attachment of the spermatophore. Females of *A. domesticus* are unreceptive for 6–9 days following eclosion, which is longer than the period following eclosion in

which they are unresponsive to male acoustic signals (142). Commonly, unreceptive females display vigorous rejection behavior in response to male courtship and, particularly, to attempts at copulation. Behavior of this kind is exhibited, for example, by the acridids *C. curtipennis* (78) and *S. gregaria* (173) and the blowfly *L. cuprina* (6). Such behavior is displayed by the acridids for several days after eclosion. In *L. cuprina*, the development of sexual receptivity depends on diet. The majority of females fed only sugar and water continue to reject attempts at copulation for at least 9 days after eclosion, whereas they become receptive within 48 h of ingesting protein-rich material required for ovarian development (9).

As is the case with the ontogeny of calling behavior, the development of receptive behavior is under the control of hormones in some species and not in others. Examples of species in which the development of receptivity is under the control of juvenile hormone appear in reviews by Barth & Lester (7) and Truman & Riddiford (183). More recently, evidence has been obtained for the involvement of this hormone in the development of receptivity of additional species including the locust *S. gregaria* (173) and the blowflies *L. cuprina* (9) and *Calliphora vomitoria* (180). The crickets *Teleogryllus commodus* (105) and *Gryllus bimaculatus* (122) are insects in which the development of receptivity does not appear to be under hormonal control. In another cricket, *A. domesticus*, juvenile hormone is involved in the development of the response of females to male acoustic signals (94), but evidence is conflicting about its role in the development of receptivity to male courting (130, 171).

MALES   As with females, males of many species do not display sexual activity for some days after eclosion. For example, the interval between eclosion and the time at which males first direct sexual behavior towards the female is about 1 day in *Drosophila melanogaster* (65), 5 days in the milkweed bug, *O. fasciatus* (106), and ranges from about 5 days to more than a week in some acrid species (39, 47, 124, 125). Physiological mechanisms controlling the development of male sexual behavior have been most extensively studied in acridids (see 124, 125 for review). These studies have shown that juvenile hormone is involved to varying degrees in some species but not at all in others. Several studies have investigated the effects on the development of sexual behavior of removing all or part of the male reproductive system. Removal of the testes of *O. fasciatus* (106), testes and reproductive accessory glands of *L. migratoria* (47), and reproductive accessory glands of *Melanoplus sanguinipes* (39) does not inhibit the development of sexual behavior.

Males of *Gryllus pennsylvanicus*, *G. integer*, *G. veletus*, and *Teleogryllus africanus* first produce acoustic signals on day 4 after the imaginal molt, and the calling time per night increases up to day 6 (30). Males of another cricket,

Gryllus campestris, call only when they are carrying a spermatophore (151). However, calling in *G. pennsylvanicus, G. integer, G. veletus,* and *T. africanus* begins 1–2 days before the formation of their first spermatophore (30), which suggests that the failure of the young adults to call cannot be attributed to the lack of a spermatophore alone.

The age at which males of noctuid moths first become responsive to the sex pheromone of the female ranges from 1 to 3 days (148). Males of the cockroach, *Periplaneta americana,* do not show all behavioral elements of the response to pheromone until about 2 weeks after the imaginal molt; the order in which the various elements appear after eclosion is the same as that in which they are displayed, in mature males, in response to progressively higher pheromone concentrations (149).

Mating History

The mate-oriented behavior of an individual can be affected by its mating history. In several species, mating is followed by a period during which the likelihood that further matings will occur is reduced, and the effects in females are generally more pronounced than those in males.

FEMALES   Females of some species, for example the cricket *G. bimaculatus* (150) and psyllid *Cacopsylla pyricola* (95), mate several times per day, but females of most species mate much less frequently. The housefly *M. domestica* (135), the blowfly *L. cuprina* (166), and the leafminer *A. frontella* (35) probably mate only once or twice in their lives. Females of other species, such as *D. melanogaster* (181) and *Hylemyia brassicae* (175), mate somewhat more frequently, but successive matings are separated by one or more days. The basis for relatively infrequent mating is that a period follows mating during which there is a low probability that females will mate again. As in young females, failure to remate can result from either lack of courtship by the male or failure of the female to display receptive behavior, or both.

Mating can inhibit release of sex pheromone. Among lepidopterans, for example, females of *M. sexta* do not call for 7–9 days after mating (144), and those of *Mamestra configurata* do not do so for 1–4 days (81). Females of the cockroach *S. longipalpa,* once mated, never resume calling (165). Mating has also been shown to suppress pheromone synthesis in some lepidopterans. For example, females of *Heliothis virescens* have low pheromone content for two days following mating (127) and those of *L. dispar* for at least 5 days (68). In *D. melanogaster,* a species in which sex pheromone is present on the cuticle surface, males direct less courtship toward mated than toward virgin females. This reduction in courtship results from synthesis by the mated female of cuticular hydrocarbons that are present on the cuticle

of the mature male (145, 147). Males are stimulated less by odor of mated *L. cuprina* females than by that of virgins (6), but the basis for the reduction is unknown. Failure to release pheromone and the presence of antiaphrodisiacs both decrease the likelihood that males will interfere with females that are engaged in other behaviors.

Effects of mating on the responses of females to male-produced stimuli have received considerable attention, but space constraints allow only a few aspects to be mentioned here. Mating reduces the responses of females to male-produced acoustic signals (e.g. 94, 114) and male pheromone (e.g. 63, 88), and increases the likelihood that a female will display some kind of rejection behavior when courted by males or when copulation is attempted (e.g. 166).

The period for which females remain unreceptive following mating can be affected by oviposition: the return of receptivity after mating is accelerated by oviposition in several species including the dipterans *M. domestica* (135), *Culex tarsalis* (202), *L. cuprina* (166), and *D. melanogaster* (181) and in the lady beetle, *Harmonia axyridus* (117). Another factor that can affect the expression of mating-induced loss of receptivity is the recent mating history of the male with which the female has mated. In the dipterans *Aedes aegypti* (74), *M. domestica* (101), and *L. cuprina* (167), a smaller proportion of females are rendered unreceptive following matings with males that have recently mated a number of times in quick succession than following matings with males that had not mated previously or had not done so for a considerable time. In addition, those females of *L. cuprina* that are rendered unreceptive by matings with males that have previously mated repetitively tend to show a more rapid return of receptivity (167).

Several factors associated with mating are involved in the mating-induced loss of sexual receptivity in females. Prominent among these are mechanical stimulation received during copulation (e.g. 71), distension of the bursa copulatrix (e.g. 103, 141), the presence of sperm in the spermatheca (e.g. 109), and the action of the products of male accessory reproductive glands in the females (see 40, 70, 100, for reviews). More than one factor can contribute to the postmating loss of receptivity, and different factors can become operative at different times after mating. In the tsetse *Glossina morsitans*, physical stimuli are responsible for a short-term reduction in the likelihood that a female will remate, and accessory-gland material is responsible for a long-term complete loss of receptivity that does not develop fully until 5 days after copulation (71). In *D. melanogaster*, accessory-gland peptides are responsible for short-term effects and sperm in the spermatheca for a longer-term reduction in receptivity (146). Similarly, the postmating suppression of pheromone synthesis is a two-stage process in *L. dispar* (69) and *S. longipalpa* (165).

MALES   The frequency with which males mate when given effectively unlimited access to receptive females varies widely between species. Males of some insects will mate many times a day. For example, previously unmated males of the blowfly *L. cuprina* can mate an average of 10 times and up to 23 times in a day and continue to mate at high frequency on at least the following day (167), and males of the cricket *G. bimaculatus* can mate at hourly intervals (115). In contrast, males of the katydid *Requena verticallis* mate only about 5 times in 17 days, with intervals lasting some days between matings (75). Variation between species as regards the mating frequency of males indicates that there are differences in the period following copulation in which males are unresponsive to stimuli from females.

The physiological basis for the postcopulatory refractory period in males has not been fully elucidated in any insect. However, indirect evidence in some crickets and katydids indicates that the postmating refractory period is associated with the need for replenishing stores of the accessory reproductive gland material required for spermatophores and seminal fluid (75, 143, 151). However, males of some other species including the monarch butterfly, *Danaus plexippus* (118), and the blowfly *L. cuprina* (167) continue to mate quite readily even though they are able to transfer only a smaller spermatophore, a lesser amount of seminal fluid, or a smaller number of sperm than is transferred by males that have not mated recently.

OVIPOSITION SITE–ORIENTED BEHAVIOR

Oviposition-site–oriented behavior is also affected by endogenous factors. I consider only two of these. The first comprises effects correlated with, but not necessarily causally related to, the condition of the ovaries, and the second is the mated status of the female. Experience can also modify oviposition behavior, especially choice of oviposition site (see 123, 190 for review).

Effects of Ovarian Condition

Females of some species display distinct ovarian cycles in which batches of oocytes in the individual ovarioles develop synchronously; maturation of the next batch of oocytes is inhibited until the previous batch is laid. Typically, females with this type of ovarian development lay their entire complement of mature eggs in a single bout of oviposition. Females with ovarian development and oviposition behavior of this kind have batches of similar numbers of eggs available for laying at more or less regular intervals. When females with mature oocytes are prevented from ovipositing, the number of oocytes does not increase with time. The ovarian development and/or oviposition behavior of females of other species results in their carrying different numbers of eggs at different times, with egg-load usually increasing during periods of